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Published in:
Applied Animal Behaviour Science

DOI:
10.1016/j.applanim.2017.02.002

Print publication: 01/06/2017

Document Version
Peer reviewed version

Aggressive behaviour at regrouping is a poor predictor of chronic aggression in stable social groups

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Abstract

Commercial pigs globally are routinely mixed into new social groups. This results in regrouping aggression predominantly during the first 24h which compromises welfare and productivity. Chronic aggression persists thereafter and is also undesirable. Management strategies are needed that reduce the costs of aggression in both of these contexts. Pigs vary greatly in aggressive behaviour and numbers of skin lesions. This study examined how regrouping behaviour affects immediate and long-term lesion counts with a specific focus on understanding the behaviour of pigs with few lesions in both social contexts. Aggressive behaviour from 1163 growing pigs was observed for 24h post-regrouping and fresh lesions were counted 24h and 3 weeks post-regrouping. Similarity between pigs was calculated using all behavioural traits recorded during the 24h post-regrouping. Clusters of pigs were formed using furthest neighbour clustering with a stopping rule of 80% similarity. Five clusters of pigs representing 90% of the population (1047 pigs) were identified. For each regrouping aggressive behaviour trait and for fresh lesion counts 24h post-regrouping the means differed significantly ($P<0.0001$) between clusters. The most extreme clusters were characterised by extremely high or low levels of aggression with the other three clusters characterised by pigs that were unaggressive losers, selectively aggressive or with long fights. Statistically significant ($P<0.05$ – $P<0.001$) but numerically small differences between clusters were found in lesion count 3 weeks post-regrouping. Pigs were separately categorised based upon their combination of lesion counts recorded 24h and 3 weeks post-regrouping. Pigs showing similar behaviour at regrouping displayed wide ranging combinations of acute and chronic lesion outcomes. Pigs with particularly low lesion counts at both regrouping and 3 weeks post-regrouping were found in all 5 clusters. Avoidance of aggressive behaviour at regrouping resulted in few lesions at 24h but more lesions at 3 weeks. Increasing the proportion of pigs in the population that receive few lesions from both regrouping and chronic aggression may require management strategies that manipulate behaviour in both contexts. Long-term costs of avoiding regrouping aggression, represented by lesion counts three weeks after re-grouping, show that regrouping aggression may retain an important function in domesticated pigs and potentially in other species.

Keywords: Aggression; pig; lesion; social; fighting; cluster analysis

1. Introduction

Aggressive behaviour is a component of the behavioural repertoire of both wild boar and commercially managed pigs. The behaviours performed are similar in these two contexts but the quantity is typically much increased under commercial production, particularly when unfamiliar animals are suddenly introduced with minimal opportunity to withdraw (regrouping; Mendl, 1995). Regrouping occurs several times in the life of most commercial pigs globally and the aggression associated with this and subsequent chronic aggression in stable social groups can be damaging even when resource needs for survival are fully met (e.g. Séguin et al., 2006; Turner et al., 2009). Regrouping aggression has deleterious impacts on animal welfare and economic productivity and has been the subject of much research to find a cost-effective method to reduce its expression. Less effort has been placed on the consequences of, and methods to control chronic aggression in stable social groups, although its welfare and economic impacts are likely to be significant (e.g. Tan et al., 1991). Management or breeding approaches that reduce the costs of aggression in both of these contexts are required.

The accumulation of skin lesions has been shown to reflect involvement in aggressive behaviour and the location of the lesions on the body allow interpretation of whether their cause was reciprocated fighting or non-reciprocated bullying (McGlone, 1985; Turner et al., 2006a). Furthermore, high numbers of skin lesions are associated with heightened plasma cortisol and metabolites indicative of muscle fatigue, a poorer growth rate, increased backfat depth, poorer food conversion efficiency, poorer meat quality and lower reproductive output (Rundgren and Löfquist, 1989; Warris et al., 1998; Turner et al., 2006b; Tönepöhl et al., 2013). As such, the reduction in skin lesions is an appropriate target to easily measure the success of management change designed to control aggression. Large phenotypic and genetic variation exists between individual pigs of the same breed managed contemporaneously under the same conditions in the number of lesions received from regrouping aggression and aggression in stable social groups (Turner et al., 2006a, 2009; Desire et al., 2015). The phenotypic correlation between the number of lesions received in these two contexts is low (Turner et al., 2009; Desire et al., 2015) and pigs therefore exist which have few lesions in both contexts, have many lesions in both contexts or which have few in one context and many in the other.

Large differences also exist between pigs in the expression of the underlying aggressive behavioural traits (e.g. Erhard et al., 1997; Turner et al., 2006a). Tönepöhl et al. (2013) and Desire et al. (2015) have shown that aggressive behavioural strategies performed at regrouping affect the accumulation of lesions at regrouping, but are also associated with the number of fresh lesions pigs continue to receive many weeks post-regrouping. The association between aggressive behavioural strategy at regrouping and long-term lesion number appears to be mostly independent of fight success and is present at both the pig and pen levels (Desire et al., 2015). However, at present it is unclear what aggressive strategy or strategies are played by pigs which accrue few lesions from both acute regrouping aggression and subsequent chronic aggression in stable social groups. This study seeks to characterise the aggressive behaviour of such pigs during the 24 hours following regrouping when aggressive social interactions are most frequent and intense. Pigs which receive few lesions under both regrouping and stable social contexts might be regarded as possessing phenotypes that would be the optimum target of management interventions designed to control aggression. This study therefore aims to provide the basic knowledge, currently lacking, of the behavioural strategies performed by these pigs during the regrouping period which may inform the management approaches that will favour the proliferation of these desirable phenotypes.

2. Methods

2.1. Ethical statement

The study was carried out in strict accordance with the recommendations in the European Guidelines for accommodation and care of animals. The protocol was approved by the SRUC Ethical Review Committee. End points were in place to prevent injury exceeding levels seen on other commercial animals housed contemporaneously on the same farm. Endpoints determined that if an animal reached this point they would be housed in a hospital pen and veterinary advice sought. No animal was hospitalised or required veterinary treatment due to aggression during the course of the study.

2.2. Animals and housing

The subjects were 1163 grower stage pigs (701 purebred Yorkshire and 462 crossbred Yorkshire x Landrace; 357 males, 119 castrates and 687 females) born and managed in 14 batches on a Swedish commercial farm. Pigs were housed in littermate groups without regrouping until 70.5 (SD 4.3) days of age and 27.6 (SD 5.6) kg bodyweight when they were regrouped into new groups of 15 using the protocol described below. The pens into which the pigs were mixed had a floor space allowance of 0.85 m^2/pig (29% slats; 71% lightly bedded solid flooring). This space allowance is considerably more generous than that required by the European Union Council Directive 2008/120/EC (0.30 m^2 per 20-30kg pig) which increased the opportunity to avoid aggressive encounters if pigs wished. *Ad libitum* dry pelleted food was provided from a single space feeder and *ad libitum* water was available from a nipple drinker. The mean ambient temperature was 19.4 (SD 2.9) °C.

2.3. Regrouping and lesion counting

Single sex and single-breed groups of 15 were formed by mixing three pigs from each of five littermate groups. As far as possible, pigs of a similar body weight were regrouped together. Immediately before regrouping, the sex, breed, litter details, pre-regrouping lesion count, and identity were recorded for each pig. After 24 h, the animals were weighed, and a post-regrouping lesion count was recorded from which the pre-regrouping lesion count was subtracted. The number of fresh lesions estimated to be within 24 hours old (fresh blood, bright red in colour or with recent and continuous scabs) was counted by a single observer throughout. Separate lesions were counted when two injuries were orientated in the same direction but separated by an approximate distance of at least 5mm of undamaged skin. Lesions were superficial and therefore severity was not recorded. Lesions to the front (head, neck, shoulders, and front legs), middle (flanks and back), or rear (rump, hind legs, and tail) of the body were recorded separately. Around 3 weeks after regrouping at 89.8 (SD 5.2) days of age, lesions were again counted on one occasion.

2.4. Behavioural recording

Pigs were video recorded for 24 hours post-regrouping and were individually identifiable by spray paint marks applied to their backs immediately before regrouping. The frequency and duration of reciprocal and non-reciprocal aggression were recorded together with the identity of the initiator and winner where these were clear. Reciprocal aggression was defined as a fight that lasted for more than one second where both pigs were involved in pushing, head knocking or biting (Turner et al., 2006a). Two severities of reciprocal aggression were separately recorded; escalated reciprocal aggression included bites delivered at a rate of at least one bite every 3 seconds while non-escalated reciprocal aggression included bites delivered at a slower rate, head knocks and pushes. The initiator of reciprocal aggression was recorded as the pig which delivered the first bite. Fight success was recorded when a pig pursued a retreating animal over a distance of at least 1 m and did not receive renewed damaging aggression from the loser for at least 3 seconds. Non-reciprocal aggression involved the delivery of escalated aggression with no retaliation from the receiver. Non-reciprocal aggression could occur as a unique event independent of a reciprocal fight, as a component of a reciprocal fight, or at the end of a reciprocal fight as the loser retreated. Three observers extracted these data from the videos. Analysis of three 1 hour samples of data showed a significant degree of inter-observer association (mean $r = 0.83$, $P < 0.001$). A large number of quantitative behavioural traits (n=31) were derived from these data to characterise a pig's involvement in, and its tendency to initiate and win aggression. These were used to study the behavioural strategies of pigs with contrasting lesion count outcomes. Table 1 lists the 10 traits most informative in characterising the behaviour of the pigs and the rationale for selecting these 10 is explained below.

Table 1. Mean expression of behavioural traits in each of the five clusters.

	Cluster 1 (n=195 pigs) 'Selectively aggressive'	Cluster 2 (n=199 pigs) 'Unaggressive losers'	Cluster 3 (n=168 pigs) 'Aggression avoiders'	Cluster 4 (n=330 pigs) 'Persistent aggressors'	Cluster 5 (n=155 pigs) 'Extreme aggressors'	SED	F statistic	Population mean (n=1047 pigs)	Population SEM
Sum of aggression									
Total duration of escalated RA[1]	5.39 (218.2)	4.87 (129.3)	1.12 (2.1)	6.18 (482.0)	6.75 (853.1)	0.09	1145	5.05 (155.0)	0.06
Total duration of RA[2]	5.59 (266.7)	5.13 (168.0)	1.23 (2.4)	6.56 (705.3)	7.18 (1311.9)	0.09	1135	5.35 (209.6)	0.07
Total frequency of RA	2.00 (6.4)	1.51 (3.5)	0.36 (0.4)	2.42 (10.2)	2.98 (18.7)	0.04	1108	1.92 (5.8)	0.03
Total duration of all interactions[3]	5.95 (382.8)	5.37 (213.9)	3.30 (26.1)	6.70 (811.4)	7.31 (1494.2)	0.07	1037	5.85 (346.2)	0.05
Total frequency of all interactions	2.72 (14.2)	2.03 (6.6)	1.48 (3.4)	2.97 (18.5)	3.51 (32.4)	0.04	691	2.58 (12.2)	0.02
Initiation and receipt of aggression									
Frequency of initiated RA	1.35 (2.9)	0.66 (0.9)	0.09 (0.1)	1.74 (4.7)	2.42 (10.2)	0.05	734	1.30 (2.7)	0.03
Total frequency of all initiated interactions	1.93 (5.9	0.93 (1.5)	0.35 (0.4)	2.28 (8.8)	2.98 (18.7)	0.05	732	1.75 (4.8)	0.03
Duration of received RA	4.76 (115.7)[a]	4.72 (111.2)[a]	0.94 (1.6)	5.72 (303.9)	6.29 (538.2)	0.10	717	4.67 (105.7)	0.06

Duration of escalated RA received	4.53 (91.8)[a]	4.46 (85.5)[a]	0.87 (1.4)	5.34 (207.5)	5.86 (349.7)	0.10	697	4.38 (78.8)	0.06
Outcome of aggression									
Duration of RA lost	3.79 (43.3)	4.56 (94.6)	0.58 (0.8)	5.51 (246.2)	5.84 (342.8)	0.11	700	4.26 (69.8)	0.06

Only the 10 traits with the highest F statistic are shown. Values presented are the natural logarithm of means (back-transformed means in parentheses). SED and SEM are estimated for $\log_e$ transformed data. Within a row, all pairwise comparisons between clusters were significant at between $p<0.05$ and $p<0.001$ unless shown by the same superscripts. All durations were measured in seconds.

[1]RA = reciprocal aggression

[2]Unless explicitly stated otherwise, 'RA' is the sum of escalated and non-escalated reciprocal aggression.

[3]All interactions' included reciprocal and non-reciprocal aggression given and received.

2.5. Statistical analysis

2.5.1. Cluster analysis of behavioural strategies at regrouping

All lesion count traits and several of the behavioural traits showed positively skewed distributions and a log transformation $Y = \log_e (1 + \text{observation})$ was used as appropriate to reduce the skewness and to satisfy the assumption of normality. A similarity matrix comparing every pig with each other was computed using all 31 behavioural traits and based on the squared Euclidean distance metric, which removes the effects of scale, thus making each behavioural variable comparable. A hierarchical cluster analysis (Genstat, 15th Edition, VSN International Ltd, UK) was undertaken. Cluster formation was based on the furthest neighbour criterion and a stopping rule of 80% similarity. Pen identity was not accounted for in the construction of the clusters as pen effects have previously been found to account for only a small proportion of the variance in skin lesions and aggressive behaviour in the same sample of pigs (0.04 to 0.13; Turner et al., 2009).

Pigs within a cluster necessarily shared similar behavioural expression on average across all traits, but cluster analysis cannot illustrate where clusters statistically differ in expression of each individual behavioural trait. To estimate how the expression of each of the 31 behavioural traits differed between the clusters, cluster means for each of the traits were compared by fitting linear mixed models using the residual maximum likelihood (REML) algorithm. Cluster identity was fitted as a fixed effect while the random effects part of the model reflected the hierarchical structure of pigs nested within pens, nested within batches of pens. Only the 10 traits with the highest F statistic indicating greatest deviation between clusters are shown in Table 1. With few exceptions, all pair-wise comparisons of clusters differed at a highly statistically significant level ($P<0.001$) with respect to all of the 31 behavioural traits. As a result, a second approach was used to identify the key behavioural traits that characterised each cluster by finding those traits expressed with greatest similarity by members of a cluster. The total variance of all standardised behavioural traits within a cluster was summed and the variance of each individual behaviour was then expressed as a proportion of the total variance of that cluster. As pigs within a cluster shared similar behavioural profiles, those behaviours that accounted for the lowest proportion of the total variance had, by definition, played the largest role in clustering the pigs together. The five traits determined on that basis to be most influential in grouping pigs into each cluster are shown in Fig. 1. The remaining 13 traits not described in either Table 1 or Fig. 1 were less informative in characterising the clusters and will not be considered further (three describing total involvement in aggression; seven describing the initiation and receipt of aggression and three describing the outcome of aggression, including whether the winner was ambiguous or clear). Differences between clusters in skin lesion count and body weight were investigated in the same manner by fitting mixed models as for the 31 behavioural traits.

2.5.2. Association between regrouping behaviour and short and long-term skin lesions

A principal aim of the study was to understand how aggressive behavioural strategies performed at regrouping resulted in contrasting skin lesion outcomes when the two contexts of regrouping and the stable social group situation were taken together. To investigate this, pigs were categorised by simultaneous reference to their lesion counts at regrouping and at 3 weeks post-regrouping relative to the population distribution for these traits. Categorising pigs by reference to both regrouping and stable group lesion counts allowed examination of both the immediate and long-term effects of different behavioural strategies performed at regrouping. Specifically, the population was divided into four categories based on quartiles of regrouping lesion counts and then further categorised based on quartiles of stable group lesion counts. In total therefore, 16 categories were formed ranging from pigs with the lowest quartile regrouping and lowest quartile stable group lesion counts through to pigs with the highest quartile regrouping and highest quartile stable group lesion counts. This categorisation was performed separately for lesions to the front of the body which primarily result from reciprocal fighting (Turner et al. 2006a) and for the total lesion count (sum of lesions to the front, middle and rear of the body). Chi square analyses were then used to determine whether behavioural clusters contained a higher or lower number of pigs from different lesion count categories than expected. The Chi square analyses used expected values based on all 16 categories but were performed only for the four most extreme combinations of regrouping and stable group lesion counts (lowest quartile – lowest quartile (LL); highest quartile – highest quartile (HH); lowest quartile – highest quartile (LH) and highest quartile – lowest quartile (HL) for regrouping and stable group lesion counts respectively). This allowed a focus on understanding how pigs with comparable lesion counts at one time point (e.g. lowest quartile at regrouping) diverged to an extreme degree at the other time point (e.g. lowest vs. highest quartile stable group lesion count). Two behavioural clusters with expected values of fewer than five pigs in any of the lesion count categories were excluded from the Chi square analyses. Significant deviations from expected numbers of pigs were identified by inspection of residuals after adjustment by the method of Haberman (1973) to have a mean of 0 and standard deviation of 1. Residuals greater than 2.0 were taken as evidence of a statistically significant difference from expected values at $P<0.05$.

3. Results

3.1. Characteristics of behavioural clusters

Seven behavioural clusters were identified by the cluster analysis but two were removed from further analysis. These two clusters contained 34 and 82 animals in total which was regarded as insufficient to study extreme combinations of regrouping and stable group lesion counts. The number of animals in the remaining clusters is shown in Table 1. No significant differences between clusters were found in body weight at regrouping (ranging from 27.0 SE 0.41 (cluster 3) to 28.4 SE 0.37 kg (cluster 5), $P>0.1$). Highly statistically significant differences were apparent between all clusters in the amount that each of the quantitative behavioural traits was expressed. Table 1 shows cluster means for the 10 behavioural traits that showed greatest difference in expression between the clusters. Out of a total of 310 possible pair-wise comparisons between clusters in expression of the 31 behavioural traits, all apart from six were statistically significant at $p<0.05$ and nine at $p<0.001$. For the suites of behavioural traits in Table 1 describing the sum of aggressive interactions or tendency to initiate aggression, differences were apparent between each of the clusters in the order 3<2<1<4<5.

Fig. 1 summarises the five quantitative behavioural traits that accounted for the lowest proportion of the total variance in behaviour in each cluster. These parameters played the largest role in categorising pigs together into a common cluster by virtue of similar behavioural expression. Traits associated specifically with involvement in non-reciprocal aggression were less influential in clustering pigs together than those associated specifically with reciprocal aggression. Three traits describing involvement in non-reciprocal aggression (number of pigs attacked, frequency of non-reciprocal aggression given and the sum of that given and received) were included in the cluster analysis, but none accounted for a low proportion of the total behavioural variance in any cluster. There was much overlap between clusters in the behavioural traits that were instrumental in clustering pigs together. For example, the total durations of reciprocal aggression and escalated reciprocal aggression both proved important in forming four of the five clusters as shown by the low proportion of total behavioural variance attributable to these traits. Clustering of pigs into Clusters 2 and 3 was based upon a more unique set of behavioural traits that focussed more specifically on the outcome of fights rather than the total quantity of fights.

[INSERT FIGURE 1 HERE]

Fig. 2 plots the duration involved in reciprocal aggression that a pig won against the duration of reciprocal aggression that the pig lost for animals in each of the five behavioural clusters. At the extremes of behavioural expression, pigs in Cluster 3 largely avoided engagement in reciprocal aggression (hereafter ‘aggression avoiders’), whilst those in Cluster 5 engaged in a median of 22 minutes (interquartile range 16.7 - 29.7) of this behaviour (‘extreme aggressors’). Inspection of Table 1 and Fig. 2 would suggest that pigs in Cluster 2 were less successful in winning reciprocal aggression than those in other clusters (‘unaggressive losers’). Pigs in Cluster 1 (‘selectively aggressive’) showed an amount of aggression similar to the population mean, but were more successful than pigs in other clusters apart from the extreme aggressors (Cluster 5). Lastly, Cluster 4 was characterised by aggressive pigs which fought for a shorter total duration than pigs in the 'extreme aggressor' cluster (5) but had fights of similar mean duration ('persistent aggressors').

[INSERT FIGURE 2 HERE]

A large number of significant differences were estimated in lesion counts at regrouping between the clusters of pigs. At regrouping, the pigs in the 'aggression avoider' cluster (3) accrued the lowest total number of lesions (mean 8.0), whilst those in the 'extreme aggressor' cluster (5) gained the highest number (mean 46.5); $p<0.001$; Table 2). This pattern was also apparent for the front, middle and rear body regions. Fewer significant differences in lesion counts 3 weeks post-regrouping were found between behavioural clusters. Pigs in the 'aggression avoider' cluster (3) had a greater total lesion count (26.3) than those in any other cluster (20.8 – 22.8; $P<0.05$). Furthermore, pigs in this cluster also had significantly more stable group lesions specifically to the front and the middle of the body than pigs in most of the other clusters ($P<0.05$), although numerical differences were small.

Table 2. Mean skin lesion counts for pigs in each of the five clusters.

	Cluster 1 (n=195 pigs) ‘Selectively aggressive’	Cluster 2 (n=199 pigs) ‘Unaggressive losers’	Cluster 3 (n=168 pigs) ‘Aggression avoiders’	Cluster 4 (n=330 pigs) ‘Persistent aggressors’	Cluster 5 (n=155 pigs) ‘Extreme aggressors’	SED	F statistic	Significance	Population mean (n=1047 pigs)	Population SEM
Lesions at regrouping										
Front	2.59 (12.3)	2.27 (8.7)	1.52 (3.6)	2.94 (17.9)	3.39 (28.7)	0.10	105.2	P<0.001	2.59 (12.3)	0.03
Middle	2.11 (7.3)^{a}	1.90 (5.7)	1.59 (3.9)	2.26 (8.6)^{a}	2.56 (11.9)	0.10	22.9	P<0.001	2.10 (7.2)	0.03
Rear	1.47 (3.4)^{ab}	1.33 (2.8)^{ac}	1.15 (2.2)^{c}	1.57 (3.8)^{bd}	1.71 (4.5)^{d}	0.09	9.6	P<0.001	1.44 (3.2)	0.03
Total	3.11 (21.4)	2.88 (16.8)	2.20 (8.0)	3.42 (29.6)	3.86 (46.5)	0.12	60.6	P<0.001	3.12 (21.7)	0.04
Stable group lesions										
Front	2.31 (9.1)^{ab}	2.31 (9.1)^{abc}	2.48 (10.9)^{c}	2.26 (8.6)^{a}	2.28 (8.8)^{ab}	0.06	5.0	P<0.001	2.31 (9.1)	0.02
Middle	2.26 (8.6)^{abc}	2.35 (9.5)^{ad}	2.46 (10.7)^{d}	2.22 (8.2)^{be}	2.20 (8.0)^{ce}	0.07	6.5	P<0.001	2.28 (8.8)	0.02
Rear	1.50 (3.5)^{a}	1.55 (3.7)^{a}	1.53 (3.6)^{a}	1.44 (3.2)^{a}	1.53 (3.6)^{a}	0.08	1.2	P=0.31	1.48 (3.4)	0.02
Total	3.13 (21.9)^{a}	3.17 (22.8)^{a}	3.30 (26.1)	3.08 (20.8)^{a}	3.10 (21.2)^{a}	0.06	5.1	P<0.001	3.13 (21.9)	0.02

Values presented are the natural logarithm of means (back-transformed means in parentheses). Within a row, all pairwise comparisons between clusters were significant at between p<0.05 and p<0.001 unless shown by the same superscripts. SED and SEM are estimated for $\log_e$ transformed data.

3.2. Composition of clusters with respect to combinations of regrouping and stable lesion counts

3.2.1. Lesions to the front of the body

For simplicity, only pigs falling into the upper or lower quartile lesion categories at both regrouping and at 3 weeks post-regrouping are described below (lowest-lowest (LL, n=85 pigs); lowest-highest (LH, n=64); highest-lowest (HL, n=71); highest-highest (HH, n=75) for regrouping and stable group lesion counts respectively). For lesions to the front of the body, the lowest lesion count quartile at regrouping ranged from 0-7 lesions and the highest ranged from 27-99 lesions. At 3 weeks post-regrouping, the lowest front lesion count quartile ranged from 0-7 and the highest from 13-63. Each of the five behavioural clusters contained pigs from all four of the lesion categories (Fig. 3) with the exception of the 'aggression avoider' cluster (3) which contained no pigs classified as HL or HH. Significantly more LL pigs were found in the 'unaggressive loser' and 'aggression avoider' clusters (2 and 3) and fewer in the 'persistent aggressor' and 'extreme aggressor' clusters (4 and 5) than expected by chance ($p<0.05$; Table 3). The same distribution was found for LH pigs except there was no statistical evidence that they were under- or over-represented in the 'unaggressive loser' cluster (2) . In contrast, HL pigs were under-represented in the 'selectively aggressive', 'unaggressive loser' and 'aggression avoider' clusters (1, 2 and 3) and over-represented in the 'persistent aggressor' and 'extreme aggressor' clusters (4 and 5). Lastly, HH pigs were under-represented in the 'aggression avoider' cluster (3) and over-represented in the 'extreme aggressor' cluster (5).

[INSERT FIGURE 3 HERE]

Table 3. Residuals of the number of pigs in each behavioural cluster according to lesion counts on the front of the body.

	Front lesion count quartile class			
Cluster	LL[1]	LH	HL	HH
1: ‘Selectively aggressive’	0.63	-0.30	**-2.59**	-1.53
2: ‘Unaggressive losers’	**2.55**	-0.05	**-3.29**	-1.60
3: ‘Aggression avoiders’	**3.81**	**8.69**	**-3.81**	**-3.93**
4: ‘Persistent aggressors’	**-3.11**	**-4.21**	**3.07**	1.64
5: ‘Extreme aggressors’	**-3.37**	**-3.07**	**6.40**	**5.36**

Positive residuals greater than 2.0 or negative residuals greater than -2.0 (in bold) were taken as evidence of a greater or lesser number of pigs respectively within a cluster than expected at $p<0.05$. The actual number of pigs with each lesion outcome present in each cluster is shown in Fig. 3.

[1]Acronyms refer to lowest (L) and highest (H) quartile lesion count at regrouping (first letter) and in stable social groups (second letter). For example, LL indicates lowest quartile regrouping and lowest quartile stable group lesions.

3.2.2. Total count of lesions to the whole body

As above, only data on pigs categorised into the lesion count quartiles LL (n=66), LH (n=63), HL (n=62) and HH (n=75) are described below. For the total lesion count on the body (sum of front, middle and rear lesions), the lowest lesion count quartile at regrouping ranged from 0-13 lesions and the highest ranged from 49-199. At 3 weeks post-regrouping, the lowest total lesion count quartile ranged from 0-16 and the highest from 33-115. Pigs from LL, LH, HL and HH lesion categories were present in all five of the behavioural clusters with the exception of HL pigs which were absent from the ‘aggression avoider’ cluster (3). The representation of these four lesion categories in the clusters (Table 4) was similar to that described above (and shown in Fig. 3) when pigs were categorised according to lesions to the front of the body. Specifically, LL and LH pigs were both over-represented in the ‘aggression avoider’ cluster (3) and under-represented in the ‘persistent aggressor’ and ‘extreme aggressor’ clusters (4 and 5). HL pigs were under-represented in the ‘unaggressive loser’ and ‘aggression avoider’ clusters (2 and 3) and over-represented in the ‘persistent aggressor’ and ‘extreme aggressor’ clusters (4 and 5). Lastly, HH pigs were under-represented in the ‘aggression avoider’ cluster (3) and over-represented in the ‘extreme aggressor’ cluster (5).

Table 4. Residuals of the number of pigs in each behavioural cluster according to lesion counts to the whole of the body (sum front, middle and rear regions).

	Total lesion count quartile class			
Cluster	LL	LH	HL	HH
1: ‘Selectively aggressive’	1.21	-0.24	-1.19	0.32
2: ‘Unaggressive losers’	1.77	0.67	**-2.93**	-1.61
3: ‘Aggression avoiders’	**2.57**	**6.33**	**-3.54**	**-2.30**
4: ‘Persistent aggressors’	**-2.14**	**-3.32**	**2.38**	-0.16
5: ‘Extreme aggressors’	**-3.14**	**-2.68**	**5.09**	**4.01**

Positive residuals greater than 2.0 or negative residuals greater than -2.0 (in bold) were taken as evidence of a greater or lesser number of pigs respectively within a cluster than expected at $p<0.05$.

[1]Acronyms refer to lowest (L) and highest (H) quartile lesion count at regrouping (first letter) and in stable social groups (second letter). For example, LL indicates lowest quartile regrouping and lowest quartile stable group lesions.

4. Discussion

4.1. Characteristics of behavioural clusters

The five clusters of pigs were formed using 31 traits describing their aggressive behaviour at regrouping. The clusters differed significantly in the quantity with which they expressed all 31 traits. The large sample size probably facilitated the identification of statistically significant differences between clusters, but inspection of the cluster means suggests that the differences were numerically large and probably biologically meaningful. This suggests that no single trait, or small number of traits, were responsible for characterising the behavioural profile of the different clusters. The behavioural traits were identified that explained the lowest proportion of the total behavioural variance within a cluster and were therefore expressed with greatest similarity by cluster members. The identified traits showed large amounts of overlap between clusters. From this, it appears that behavioural strategies of individual pigs are more easily clustered on the basis of the quantity rather than the quality of aggressive behaviour. Beyond this generalisation it was evident that the most aggressive clusters ('persistent aggressor' and 'extreme aggressor'; clusters 4 and 5) were formed due to similarities between their members in the total duration of aggressive behaviour performed, particularly reciprocal aggression. The least aggressive clusters of pigs ('unaggressive losers' and 'aggression avoiders'; clusters 2 and 3) were formed based on slightly different sets of quantitative behavioural traits associated with fight outcomes as well as the quantity of aggression *per se*. Pigs in the 'unaggressive loser' cluster (2) were the least successful in winning reciprocal aggression encounters whilst pigs in the 'aggression avoider' cluster (3) largely avoided all forms of aggression and consequently neither won nor lost fights. Evidence of pigs which successfully avoid regrouping aggression has also been presented by Camerlink et al. (2014) who reported that these pigs appear to show other alterations in their response to regrouping (greater sociality evidenced by closer spatial integration and more non-damaging social nosing).

4.2. Implications of behavioural strategies for skin lesions

Although highly significant differences in lesion counts at regrouping were apparent between clusters of pigs, fewer differences between clusters were present 3 weeks post-regrouping. Where statistically significant differences between clusters in lesion counts were identified 3 weeks post-regrouping, the numerical differences were slight. This suggests that the aggressive strategy played at regrouping has discernible but only small affects on skin lesions 3 weeks post-regrouping. This is largely in agreement with the results of Tönepöhl et al. (2013) who found evidence that some but not all aspects of aggressive behaviour of sows at regrouping affected lesion counts 10 weeks later and that these effects were restricted to lesions on the front of the body. Furthermore, no significant differences were found between clusters of pigs in the current study in the number of lesions specifically to the rear of the body at 3 weeks post-regrouping. The rump usually receives lesions during non-reciprocated bullying typical of defeat and submission (Turner et al., 2006a). The absence of an effect of aggressive behavioural strategy on these lesions suggests that receipt of chronic on-going bullying 3 weeks post-regrouping was not affected by the behaviour of pigs at regrouping, even where pigs avoided contests associated with the establishment of dominance relationships (‘aggression avoiders’; cluster 3) or tended to lose these (‘unaggressive losers’; cluster 2).

Several suggestions may be offered to explain the minor role played by regrouping aggression in determining long-term lesion outcomes. Although regrouping aggression is key to the establishment of social relationships between unfamiliar pigs, it is probable that the major determinant of fresh lesions received under stable social conditions is the proximate long-term aggressive strategy of pigs played in the weeks following regrouping. This will be partially determined by the need to compete for resources, although in the current study the floor space allowance was generous and the feeder and drinker provision complied with guidelines to industry (e.g. the feeder provision was close to that required by the higher welfare RSPCA Freedom Food scheme and drinker provision met the requirements of the UK Defra Code of Recommendations for the Welfare of Pigs). Differences in ability of individual pigs to dynamically adapt their aggressive behavioural strategy based on fight experience have been reported (Bolhuis et al., 2005) and may also explain why pigs which show similar behaviour at regrouping can subsequently diverge greatly in the number of lesions shown under stable social conditions. Aggressive behaviour performed in groups of stable composition refines and maintains previously established social relationships and is often provoked during competition for limited resources (Hagelsø Giersing and Studnitz, 1996). Other non-aggressive social behaviours, such as appeasement and social grooming, may also be influential in the long-term maintenance of these relationships (Camerlink et al., 2014) and may play a role in determining the number of lesions resulting from chronic aggression. Lastly, this study has quantified engagement in aggressive behaviour without regard to the identity of the opponent. The use of more sophisticated analytical methods such as social network analysis (e.g. Wey et al., 2008; Makagon et al., 2012; Büttner et al., 2015) to produce new quantitative measurements for each animal summarising their interactions in a complex social network could provide new insight that would help to understand the behaviour of pigs that are successful in avoiding lesions from both regrouping and chronic aggression (LL pigs).

Regrouping aggression does not appear to cluster into discrete, identifiable behavioural strategies responsible for specific combinations of lesion outcomes across social contests. For example, the aggressive behavioural strategy performed at regrouping does not explain the cause of the marked divergence of LL from LH pigs. The present analysis has examined the behaviours associated with specific combinations of lesions from these two contests with a focus on pigs with uniformly low or high lesions across the two time points (LL, HH) or those that transitioned from one extreme to the other (LH, HL). The data indicate that most behavioural clusters contained pigs with all of these lesion outcomes despite sharing greater than 80% similarity in behavioural profile in the 24 hours following regrouping. These patterns were apparent for the total number of lesions to the entire body and to those located on the front region alone which is the usual target of bites during reciprocal aggression (Turner et al., 2006a).

However, differences between clusters in the relative abundance of pigs with each lesion outcome were apparent. For lesions to the front of the body, the least aggressive cluster ('aggression avoiders'; cluster 3) contained more LL pigs than expected by chance and no HL or HH pigs. The number of LH pigs was much greater than that expected by chance suggesting that the strategy of avoiding regrouping aggression was associated with the receipt of many lesions 3 weeks post-regrouping.

Lesions to the front of the body tend to result from engagement in reciprocal fighting rather than receipt of bullying (Turner et al., 2006a). As a result, these LH pigs that were unaggressive at regrouping appear to have shown significant amounts of reciprocal aggression in the following weeks. Evidence from rats suggests that experience of fighting, even when this leads to defeat, can reduce the amount of aggression received by animals when they subsequently meet unfamiliar individuals (Lehner et al., 2011). This, together with the current data, may indicate that there is a long-term cost to avoiding aggression. The most aggressive cluster ('extreme aggressors'; cluster 5) contained fewer LL pigs than expected and more HL and HH pigs. As a cluster, these pigs were the most successful at winning encounters at regrouping compared to pigs in other clusters (except the 'selectively aggressive' cluster (1)) and, as such, may be expected to have attained the highest dominance rank. If this is the case, it is perhaps unsurprising that this cluster contained many HL pigs. However, it is interesting that it also contained a disproportionately high number of HH pigs which continued to receive many fresh lesions to the front of the body 3 weeks post-regrouping, long after dominance relationships should have been formed. Potentially these pigs received many challenges to their high dominance position requiring frequent reciprocal aggression or they were simply more aggressive pigs as a result of genetic and lifetime experiential effects. The patterns described above were very similar for the total lesion count.

4.3. Implications for management

Reducing aggression at regrouping and in stable social groups implies a proliferation of LL pigs in the population. As all behavioural clusters contained LL pigs, favouring the production of LL pigs through management or breeding is unlikely to eliminate from the population any aggressive strategy identified in this study. The only aggressive behavioural strategy which was associated with a greater likelihood of an LL outcome was that displayed by the 'aggression avoider' cluster (3), characterised by the total avoidance of reciprocal aggression at regrouping. However, this strategy also resulted in many LH pigs and a total lesion count 3 weeks post-regrouping that was significantly higher than for any other cluster. It has been suggested previously (Mendl and Erhard, 1997; Turner et al., 2010) that an unwillingness to fight may result from high levels of fear and therefore measures of affective state of pigs of different aggressive strategy, and lesion outcomes would be particularly valuable in guiding effort to better control aggression and improve welfare. To understand how injuries at regrouping and in later stable groups compare in their effects on welfare it would also be beneficial to identify any difference in severity of lesions at these two time points, as well as the number of lesions as here.

Management strategies which focus solely on minimisation of aggressive behaviour at regrouping appear unlikely to benefit the number of lesions pigs receive in the longer-term. The simultaneous reduction in aggression in these two social contests is likely to require the direct and simultaneous targeting of lesion count at both time points through appropriate management change. The phenotypic correlation between lesion counts at regrouping and 3 weeks post-regrouping is significant but low (Turner et al., 2009; Desire et al., 2015). However, larger genetic correlations have been estimated between lesion counts in these two contexts (Turner et al., 2009). This suggests that management change and breeding to reduce aggression in one social context (regrouping or stable social groups) will have different impacts on the other context. Unlike management change, selective breeding for a low lesion count in only one context may achieve a simultaneous reduction in lesions in the other context without requiring the recording of lesion counts in both situations.

5. Conclusions

Aggressive behaviour at regrouping and subsequently under conditions of stable group composition are affected by different motivational drivers (Hagelsø Giersing and Studnitz, 1996), despite sharing some commonality in genetic determination illustrated by their genetic correlation. Aggression in both contexts is unlikely to respond simultaneously to a management intervention made under only one of these contexts. Practical and economic constraints limit opportunities to reduce lesions from aggressive behaviour. At present it is unknown how a reduction in the high number of lesions received over a short period at regrouping would compare in welfare and economic impacts to a reduction in the lower number of lesions received over a longer period in stable social groups. Work to understand where effort is best targeted to maximise welfare and economic gains would be beneficial. Evidence that avoidance of regrouping aggression results in a higher number of lesions from chronic aggression whose location indicates involvement in reciprocated aggression shows that regrouping aggression may retain a function in domestic pigs. This may have implications for other species where regrouping aggression occurs and effort is made to reduce its expression.

Acknowledgements

We acknowledge the help of SRUC technical staff for managing data extraction and handling. N Lundeheim, L. Rydhmer, B. Olsson and U. Schmidt are thanked for input to experimental design and primary data collection. The help of staff on the commercial farm where data were collected is gratefully acknowledged. This work was partly funded by the Scottish Government's Rural and Environment Science and Analytical Services Division (RESAS).

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Fig. 1. Percentage of total behavioural variance explained by quantitative behavioural traits for each of the five clusters (C1-C5) of pigs. For clarity, only the five behavioural traits per cluster are shown that accounted for the lowest percentage of the total behavioural variance as these contributed most to clustering pigs together based on similarity of behavioural expression. RA = reciprocal aggression.

Fig. 2. Distribution of pigs from each of the five behavioural clusters with respect to the duration of reciprocal aggression won (sec; X axis) and the duration of reciprocal aggression lost (sec; Y axis).

Fig. 3. The number of pigs from each behavioural cluster that displayed extreme combinations of lesion counts to the front of the body at regrouping and 3 weeks post-regrouping (stable group). Acronyms refer to lowest (L) and highest (H) quartile lesion count at regrouping (first letter) and in stable social groups (second letter). For example, LL indicates lowest quartile regrouping and lowest quartile stable group lesions.